Visually assessed body condition shows high heritability in a pedigreed great ape population

Body condition shows high heritability in a pedigreed great ape population

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Running title: Bonobo body condition is heritable

Abstract

Body condition, a measure for relative fat mass, is associated with primate health, fitness, and overall welfare. Body condition is often influenced by dietary factors, age, and/or sex, but several body condition measures (body weight, weight-to-height ratios, etc.) also show high heritability across primate species, indicating a role of genetic effects. Although different measures for body condition exist, many require direct handling of animals which is invasive, time-consuming, and expensive, making them impractical in wild and captive settings. Therefore, non-invasive visual body condition score (BCS) systems were developed for various animal species, including macaques and chimpanzees, to visually assess relative fat mass. Here, we evaluate the utility of a visual BCS system in bonobos by assessing (1) inter-rater reliability, (2) links with body mass, a traditional hands-on measure of condition, and (3) the factors driving individual variation in BCS. We adapted the chimpanzee BCS system to rate 76 bonobos in 11 European zoos (= 92% of the adult population). Inter-rater reliability was high (s* = 0.948), BCSs were positively associated with body mass (β = 0.075), and not predicted by diet, sex, or age, nor were they associated with a higher abundance of obesity-related diseases. Instead, BCSs showed high levels of heritability (h^2 = 0.637), indicating that a majority of body condition variation in bonobos is attributable to genetic similarity of the individuals. This is in line with reported h^2-values for traditional body condition measures in primates, and provides support for the reliability of visual BCS systems in great apes. The results of this study emphasize an often unanticipated role of genetics in determining primate body fat and health that has implications for the management of captive primates. Application of this tool in wild populations would aid to unravel environmental from genetic drivers of body condition variation in primates.

Key-words: bonobo, body condition score, relative fat mass, animal models

Abbreviations:

- BCS = Body condition score
- BIC = Bayesian information criterion

- BMI = Body Mass Index
- h^2 = narrow-sense heritability
- HPD = Highest-posterior-density
- MCMC = Markov chain Monte Carlo
- V_A = additive genetic variance
- V_P = total phenotypic variance
- WHI = Weight-to-height index
- ZIMS = Zoological Information Management Software

Introduction

Body condition, a measure reflecting the energy reserves or relative fat mass of an animal (Peig & Green, 2009), is an important indicator of fitness and welfare in various non-human primate species. Good body condition (i.e., healthy amounts of fat mass) is often associated with higher reproductive success (e.g., in wild golden lion tamarins (*Leontopithecus rosalia*): Bales et al., 2001; in captive rhesus macaques (*Macaca mulatta*): Bercovitch et al., 1998; in wild Verreaux's sifakas (*Propithecus verreauxi*): Richard et al., 2000; in wild Hanuman langurs (*Presbytis entellus*): (Koenig et al., 1997)) and increased survival (e.g., in captive rhesus macaques: Mattison et al., 2017; in captive grey mouse lemurs (*Microcebus murinus*): Hämäläinen et al., 2014). On the contrary, obesity (i.e., fatness exceeding normal boundaries for the species), which often occurs in non-human primates (hereafter: primates) under human care, might lead to adverse health effects, such as increased occurrence of diabetes, cardiovascular diseases, and hypertension (e.g., in captive chimpanzees (*Pan troglodytes*): Ely et al., 2013; Obanda et al., 2014; in captive long-tailed macaques (*Macaca fascicularis*): Young et al., 2003), or even higher mortality (e.g., in captive orangutans (*Pongo* spp.): Cocks, 2007). Poor body condition in primates can also be caused by disease (e.g., in wild chimpanzees: Terio et al., 2011), severe stress (e.g., in wild vervet monkeys (*Cercopithecus aethiops*): Suleman et al., 2000) or old age (e.g., in captive great apes: Lowenstine et al., 2016), leading to higher mortality and lower reproductive success in underweight individuals. Hence, the monitoring of body condition is an important part of evaluating primate fitness and welfare.

Body mass is often used as a proxy for body condition. However, while body condition pertains to the nutritional state of the animal, body mass does not always reflect the amount of subcutaneous fat of an individual, as it does not take into account variation in body frame size or body composition (e.g., fat mass relative to muscle mass). This caveat has been solved by the introduction of several alternative, but more complex, measures for body condition. In humans and non-human primates, weight-to-height index (WHI) measures, such as the body mass index (BMI) measure in humans, have

been developed as a more accurate description of body condition (e.g., Kavanagh et al., 2007; Sterck et al., 2019). However, while accounting for stature, these WHI measures do not always provide information on overall body composition or 'fatness' and might still lead to misclassifications (Lee et al., 1982), for example when individuals with high muscle mass show high WHI-measures and are consequently falsely considered to have high relative fat mass. To develop accurate WHI-measures that correctly reflect body condition, additional information is needed on body composition (e.g., Sterck et al., 2019), which can be obtained through sophisticated techniques such as magnetic resonance imaging, dual energy X-ray absorptiometry, or skinfold measurements (e.g., Colman et al., 1999; Ellis et al., 2000; Kemnitz & Francken, 1986). While all these measurements provide a reliable and complete picture of body condition, especially in combination with mass and height measurements, they are also invasive, expensive, time-consuming, and often require sedation of animals. This renders them impractical for use in primates, especially when repeated, longitudinal measurements are needed.

To circumvent these issues, body condition scoring systems have been developed for domestic mammals (e.g., in cats and dogs: German et al., 2006; in livestock: Domecq et al., 1995), but also for wild and captive non-domesticated animals such as different ungulate species (e.g., Alapati et al., 2010; Clavadetscher et al., 2021; Ezenwa et al., 2009; Heidegger et al., 2016), elephants (e.g., Fernando et al., 2009; Morfeld et al., 2016) and primates (e.g., Clingerman & Summers, 2005; Reamer et al., 2020). These body condition scoring system are often based on a visual and palpatory examination of the animal, but purely visual body condition score systems have also been developed as these are more practical for use in non-domestic animals (Schiffmann et al., 2017). These visual body condition score (BCS) systems are based on a visual inspection of the body condition focusing on specific body parts , such as abdomen curvature, thickness of legs, or the visibility of certain skeletal features. These body parts or regions can be scored separately and summed to obtain the BCS for that individual, or a body condition score can also be given through an overview BCS system, focusing on a 'general impression' of the body condition of the animal (Schiffmann et al., 2017). This way, each individual's body condition

can be scored on a scale from “underweight” through “normal” to “overweight” or “obese”. The development of a visual BCS system for a certain taxon requires validation through measurements of body composition, such that the BCS system accurately reflects body condition. In primates, a visual BCS system was developed for macaques which correlates with body fat (Berman & Schwartz, 1988; Clingerman & Summers, 2012; Summers et al., 2012). This system was later on adapted to score the body condition of chimpanzees (Reamer et al., 2020). These BCSs systems showed high inter-observer repeatability, underlining their reliability, and they offer a practical tool for non-invasive evaluation of the body condition of primates.

In many studies, large between-individual variation in BCS is reported, which has been linked to dietary factors in some cases. For example, in zoo-housed tapirs, higher BCSs correlated with higher digestible energy intake (Clauss et al., 2009), while in rhinoceroses, higher quantities of food offered led to higher BCSs (Heidegger et al., 2016). However, diet alone does not account for all variation seen in BCSs among animals, as individuals housed in the same institute receiving the same diet still show variation in BCSs (e.g., in chimpanzees: Reamer et al., 2020). This indicates that other factors are at play, independent of dietary effects. Age- and sex effects in body condition scores have been found in various animal species (e.g., Clavadetscher et al., 2021; Morfeld et al., 2016), including rhesus macaques (Clingerman & Summers, 2005) and chimpanzees (Reamer et al., 2020), with female chimpanzees having higher BCSs than males, and an increase is found in BCSs with age. Geriatric great apes, on the other hand are expected to show lower BCS, as they generally lose mass in old age (reviewed in Lowenstine et al., 2016).

Moreover, primates may have genetic predispositions towards low or high levels of subcutaneous fat, creating variation in BCSs among individuals that is relatively independent of other environmental or intrinsic effects. This might explain why some individuals have been observed to ‘spontaneously’ develop obesity, even under standardized conditions (e.g., in baboons (*Papio anubis* and *Papio cynocephalus*): Comuzzie et al., 2003; in rhesus macaques: Kemnitz & Francken, 1986; in

Japanese macaques (*Macaca fuscata*): Takahashi et al., 2006). Different body condition measures like body mass, fat mass, and WHI have indeed shown significant levels of relatively high heritability ranging from 0.40 to 0.72 across primate species, meaning that a significant proportion of the observed variation in body condition measures in the population is explained by the genetic relatedness between the individuals, and thus explained by genetic similarities. Pure body mass shows moderate to high heritability in different primate species (h^2 = 0.80 in captive baboons (*Papio* spp.) (Cai et al., 2004); h^2 = 0.72 in captive vervet monkeys (Schmitt et al., 2018); h^2 = 0.62 in male captive baboons (Comuzzie et al., 2003); h^2 = 0.50 in captive baboons (Jaquish et al., 1997); h^2 = 0.43 in captive baboons (Joganic et al., 2018); h^2 = 0.40 in semi-wild rhesus macaques (Kimock et al., 2019)), while measures of body composition such as fat mass or skinfold measurements are heritable in male captive baboons (h^2 = 0.41 (Comuzzie et al., 2003)) and semi-wild rhesus macaques (h^2 = 0.51 (Kimock et al., 2019)). WHI-measures show heritability in captive vervet monkeys (h^2 varies from 0.44 (Kavanagh et al., 2007) to 0.65 (Schmitt et al., 2018)) and captive baboons (h^2 = 0.43 (Cai et al., 2004)), and in humans (h^2 of BMI ranges between 0.24 to 0.90, reviewed in Elks et al. (2012)).

To the best of our knowledge, studies investigating heritability of BCSs have not included primates, but were mostly performed using domesticated species such as cows (*Bos taurus*), sheep (*Ovis aries*), and pigs (*Sus domesticus*), often in a context to maximize productivity using selective breeding. Heritability of BCSs in domestic mammals varies widely between 0.10 and 0.66, depending on species, breed, sex, and age (e.g., Arango et al., 2002; Berry et al., 2002; Borg et al., 2009; Dal Zotto et al., 2007; Dechow et al., 2001; Fernandes et al., 2015; Johnston et al., 1996; Kadarmideen & Wegmann, 2003; Lundgren et al., 2012; Martinsen et al., 2016; Mirza et al., 2013; Sánchez-Guerrero et al., 2019; Tait et al., 2018; Toshniwal et al., 2008; Veerkamp et al., 2001). Assessments of BCSs in domesticated species are typically also done in combination with palpation, which might be more accurate than purely visual BCSs used in non-domesticated species. Studies assessing the heritability of BCSs in non-domesticated animal species are rare. In a captive population of arctic foxes (*Vulpes lagopus*), bred for their pelt, the heritability of BCS was moderate at h^2 = 0.30 (Kempe et al., 2010), but

still with genetic influences dominating over any litter effects (i.e., maternal effects). In other captive animal species that are not used for economic benefits, such as zoo-housed primates, the heritability of BCSs has not been evaluated yet. Moreover, to our knowledge, the heritability of any measure of body condition has not been evaluated in great apes, except for humans. Nonetheless, we expect to find significant heritability in primates as well, in line with findings in domestic animals.

In this study, we aim to evaluate the utility of a visual BCS system in zoo-housed bonobos (*Pan paniscus*) by assessing (1) the inter-rater reliability, (2) links between visual BCSs with body mass, a more traditional hands-on measure of body condition, and (3) the factors driving individual variation in BCSs. To do so, we assess the reliability of a visual BCS system originally developed for chimpanzees (Reamer et al. 2020), as no formal visual BCS system has been developed for bonobos. We used the chimpanzee BCS system as bonobos and chimpanzees are closely related sister-species with highly similar body builds. While bonobos are traditionally described as more gracile and slender than chimpanzees, with longer and heavier hindlimbs (Zihlman & Cramer, 1978), the differences between the species might actually be more subtle and they are now considered to be morphologically similar (Druelle et al., 2018). For the bonobo BCS system to be reliable, we expect that bonobo BCSs show high inter-rater reliabilities and to be positively correlated with body mass, similar to what has been found for chimpanzee BCSs (cf. Reamer et al., 2020). To further evaluate the utility of the visual BCS system, we apply animal models to estimate BCS heritability in our population. Since BCSs represent body condition, we expect the narrow sense heritability (i.e., the fraction of phenotypic variance that can be attributed to variation in the additive effects of genes) to be in the range of previously reported primate body condition measures (h^2 varies from 0.40 to 0.80) (Cai et al., 2004; Comuzzie et al., 2003; Jaquish et al., 1997; Joganic et al., 2018; Kavanagh et al., 2007; Kimock et al., 2019; Schmitt et al., 2018). Next, we set out to investigate which additional factors explain variation in BCSs, such as sex, age, obesity-related diseases, and caloric content of the diet. Similar to what was found in chimpanzees, we predicted to find higher BCSs in female bonobos compared to males (Reamer et al., 2020), given that female bonobos tend to have higher fat mass than males (Zihlman & Bolter, 2015)

and tend to have prior access to food compared to males, which increases their chances to access preferred high-calorie foods (Vervaecke et al., 2000; White & Wood, 2007). We also predicted BCSs to increase with age, as chimpanzees show increases with age in BCSs up to 60 years old (Reamer et al., 2020), which corresponds to the age distribution in our study population. In addition, we hypothesized to find higher occurrences of obesity-related diseases like cardiovascular disease, hypertension, and diabetes in individuals with higher BCSs (Reamer et al., 2020). We also expected to find higher BCSs in zoos where animals were fed a diet high in caloric content (Clauss et al., 2009; Heidegger et al., 2016), as bonobos show body mass and energy reserve changes in response to varying energetic intake (Deschner et al., 2008).

Materials & Methods

Ethical statement

Ethical approval of this study was obtained through the Scientific Advisory Board of the Royal Zoological Society of Antwerp and the University of Antwerp (Belgium) (Ref.: EC-5/SGZ(08-12-20)). All bonobos were housed according to EAZA guidelines and our research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates and the European Directive 2010/63.

Study population

This study was conducted on the entire European population of zoo-housed bonobos (*Pan paniscus*) between 2021 and 2022 aged 12 years or older (cf. Reamer et al., 2020), as bonobo body size and weight stabilize around this age (Berghänel et al., 2023). All animals were housed in multi-male multi-female groups. Females that were past the first trimester of pregnancy (i.e., pregnant for longer than 80 days (Drews et al., 2011)) or that continuously carried a dependent infant on the abdomen were excluded, as this complicates the reliable estimation of BCSs. The remaining sample included 76 animals (92% of the entire European zoo-housed bonobo population ages 12 years and older; $N_{females}$

= 48, N_{males} = 28; age range: 12-70 years) from 11 zoological institutions (see Supplementary Dataset 1).

Body condition score assessment

Body condition scores (BCSs) were assessed using the visual BCS system for chimpanzees developed by Reamer et al. (2020). This scoring system is based on giving each individual ape a rating on a scale going from 1 ("emaciated") through 5 ("normal") to 10 ("extremely obese") (see Supplemental Figure S1, figure was adapted from Reamer et al. (2020)). We collected 'in-group BCSs', meaning that BCSs were assessed when animals where freely moving in their enclosures, such that all data could be collected non-invasively. Short videos of about 10-15 seconds were made using a video camera (Legria HFR88, Canon, Tokyo, Japan) in side-view of walking bonobos from the visitor area (see Supplemental File S1 for an example video; see Figure 1). BCSs were assessed based on these videos by four raters independently, with one video rated per individual bonobo. All four raters were behavioral biologists that have worked with bonobos for at least two years. Ratings were afterwards tested for interobserver reliability, to assess reliability of the use of the chimpanzee BCS system in bonobos (see "Statistical Analysis").

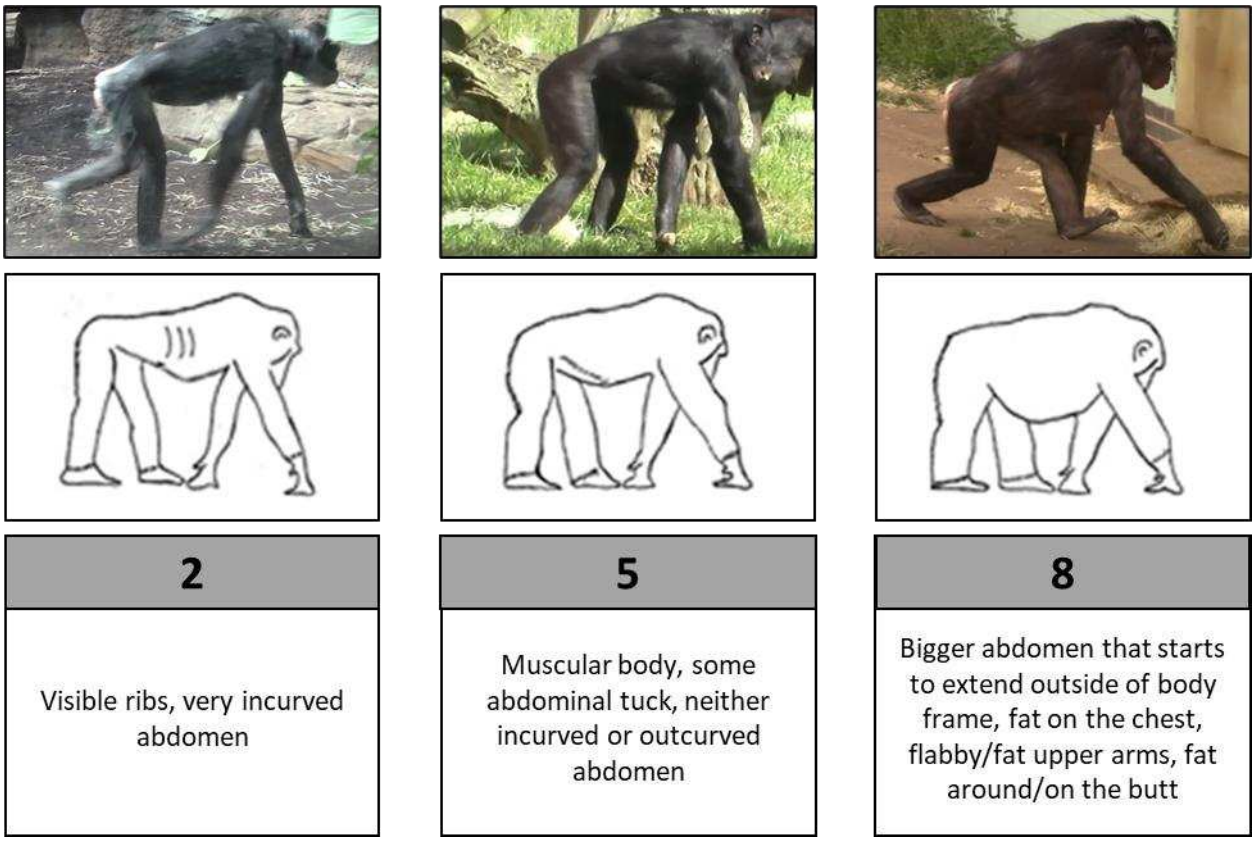

Figure 1: Excerpt from the visual body condition score system with example frames from the videos used to score the body condition. Each BCS category on the scoring sheet was accompanied with a standardized illustration and an explanation. See Supplemental Figure S1 for the full BCS system as used in this study.

Metadata collection

Data on sex, age, and kinship were collected from the Bonobo International Studbook (Stevens et al., 2022). Both sire and dam were known for each bonobo born in captivity, and wild-born bonobos were considered to be founders and thus to be unrelated to other wild-born bonobos. Data on the occurrence of obesity-related disease, body mass during the data collection, and diet were obtained through questionnaires and usage of the Zoological Information Management Software (ZIMS) database. Our selection of obesity-related diseases is based on those investigated in chimpanzees by Reamer et al. (2020), and included hypertension, diabetes, arthritis, and cardiovascular disease. In our study population, only the occurrence of cardiovascular disease was reported, with no known cases of

hypertension, diabetes, and/or arthritis. Hence, each bonobo was given a score of 0 (no cardiovascular disease reported; $N_{healthy}$ = 71) or 1 (cardiovascular disease reported; $N_{cardiac}$ = 5). Cardiovascular disease was screened using stethoscope checks, radiographs and/or echocardiograms (see Supplementary Dataset S1). These five individuals with reported cardiovascular disease lived in three different zoos, with three of the five being related as they represent a mother and her two adult sons. For body mass, we included the most recent body mass (in kg) in case it was measured within three months before or after BCS assessment. This resulted in body mass data for 40 bonobos (52% of the study sample; $N_{females}$ = 24, N_{males}= 16, age range: 12-58 years). To estimate the caloric content of the provided diet ("provided calories" from here on), dietary overviews were provided by each zoological institute which contained listings of separate food items and the quantity given of these food items. Three out of the 11 zoos had no fixed dietary item list, and were therefore excluded from further analyses involving dietary data, reducing the sample size to 61 bonobos from eight groups ($N_{females}$ = 39, N_{males}= 22, age range: 12-58 years) for these analyses. To estimate total provided calories, we calculated the average portion of a food item given in a zoo (g/day/individual) and then multiplied it by its energy content (kcal/g), obtained from the McCance and Widdowson's The Composition of Foods Integrated Dataset 2021 (Public Health England, 2021) or from the manufacturer in case of branded foods such as primate pellets, to get the daily amount of calories provided (kcal/day/animal) of that certain food item. Then, the total average daily provided calories was determined by calculating the sum of the daily provided calories of all separate food items, leading to a value for the total provided calories (total kcal/day/animal) for each zoo. Estimated provided calories from the diet sheets varied between 855 and 2825 kcal/day/animal. Browse was not incorporated into this calculation as zoos did not have information on the consumption of this dietary item. Browse was available *ad libitum* in the outdoor area of certain zoos, or was provided to the bonobos by the keepers according to availability. Supplementary Table S1 provides an overview of all metadata.

Statistical analysis

All statistical analyses were performed in R v.4.1.1 (R Core Team, 2022).

Inter-observer reliability of BCSs

To test whether BCSs could be reliably estimated from our videos, inter-observer reliabilities were assessed by calculating the s* measure. The s* measure is a modified Fleiss kappa statistic measure, which is more reliable than the traditional Fleiss' kappa measure when dealing with ordinal data assessed by multiple raters (Marasini et al., 2016) and varies between 0 and 1, with 1 indicating full agreement among observers. The s* measure was calculated using the wquad.conc function from the *raters* package (Quatto & Ripamonti, 2022). This function also allows for significance testing and the construction of 95% confidence intervals of the s*-measure through Monte Carlo procedures. If inter-observer reliabilities showed substantial agreement (s* > 0.60) (Landis & Koch, 1977), BCSs were averaged for the same individual across the four raters for further use in analyses.

Correlation between BCSs and body mass

To assess whether BCSs are related to body mass, we constructed linear mixed models with BCSs as the response variable and sex, body mass, and their interaction as explanatory variables using the *lmerTest* package (Kuznetsova et al., 2017). Group was added as a random intercept to account for non-independence of individuals housed within the same group. The Shapiro-Wilk normality test (Shapiro & Wilk, 1965) and diagnostic plots (residuals vs. fitted values and QQ plots) showed no violations of the assumptions of normality and homogeneity of variances. Backwards selection was used to identify significant factors, with α set at 0.05.

Description of BCSs in the European bonobo population

After confirming the reliability of the BCS system, we first set out to examine descriptive statistics of the BCSs in our study sample, including the mean, standard deviation, and range of the measurements. We then examined whether our population showed a tendency towards a normal level of fat mass (BCS = 5.00) using a two-tailed one-sample Student's t-Test and the Shapiro-Wilk normality test (Shapiro & Wilk, 1965). If the BCS distributions did not follow a normal distribution, and/or if the mean

289 is significantly different from a BCS of 5.00, the population tends to skew towards being under- or
290 overweight.

291 **External factors influencing BCSs and assessment of heritability**

292 To investigate which factors explain BCSs, we employed animal models implemented within the
293 *MCMCglmm* package (Hadfield, 2010). Animal models are univariate generalized mixed models that
294 allow for the assessment of the influence of genetic and environmental factors on a trait by combining
295 phenotypic and pedigree data. Thus, this approach enabled us to not only assess whether our variables
296 of interest were associated with BCSs, but we could also parse out the contribution of genetic effects
297 by calculating the narrow-sense heritability (h^2).

298 In the full model, BCSs were added as the response variable while sex (male or female), age (in
299 years), presence or absence of cardiovascular disease (yes or no) and provided calories (in kcal/day)
300 were added as explanatory variables. We ran models for 6 000 000 iterations with a burn-in period of
301 50 000 iterations and a thinning interval of 500. Priors were set at V = 1 and nu = 0.002. To verify that
302 the models met assumptions regarding autocorrelations and convergence, we inspected density plots
303 of the Markov chain Monte Carlo (MCMC) chain, verified that autocorrelations between samples were
304 less than 0.1, and ran the Heidelberg stationary test, with all p-values found to be above 0.05 (de
305 Villemereuil, 2018).

306 The significance of fixed effects was assessed from the posterior distributions using the
307 highest-posterior-density (HPD) function (Hadfield, 2010). When the HPD interval did not include zero,
308 the factor was considered significant and was kept in the model. Non-significant effects were deleted
309 from the model until only significant variables remained. Considering random effects, we included
310 identity of the animal (animal ID) to allow for h^2 assessment, mother to control for non-genetic
311 maternal effects like maternal provision of food or quality of milk (maternal ID), and group (zoo ID).
312 Maternal ID and zoo ID were only kept in the final model if they improved the DIC value of the model
313 with a ΔDIC of at least 5. Models including provided calories were run on a subset of individuals for

which detailed dietary information was available (N_{diet} = 61), while all other models were run on the full dataset (N_{full} = 76). We calculated narrow-sense heritability values (h^2) by dividing the proportion of variation due to additive genetic variance (V_A, which corresponds to the posterior distribution of the animal ID effect) by the total phenotypic variance (V_P, which corresponds to the summed posterior distribution of the other random effects (maternal effects and group effects) and the residual variance). Since the inclusion of fixed effects could inflate h^2 estimates and reduces comparability among studies (Wilson, 2008), we report h^2 estimates from a model containing random factors only, an intercept model without any factors, and from a model containing significant effects and random factors, if significant effects are found.

Results

Inter-observer reliability of BCSs

Assessing BCSs in bonobos through standardized videos showed high inter-rater reliability (s* = 0.948, 95% CI [0.934,0.961], p < 0.001). Hence, in all further analyses, BCSs were averaged for all individuals across the four raters.

Correlation between BCSs and body mass

Body mass and BCSs were positively correlated (β = 0.075, t(38) = 2.831, p = 0.007; Figure 2). There was no difference in this correlation between the sexes, as indicated by a non-significant mass-by-sex interaction (β = -0.095, t(36) = -1.288, p = 0.206), and there was no difference between the sexes in BCSs in this smaller dataset (β = -0.252, t(37) = -0.672, p = 0.506).

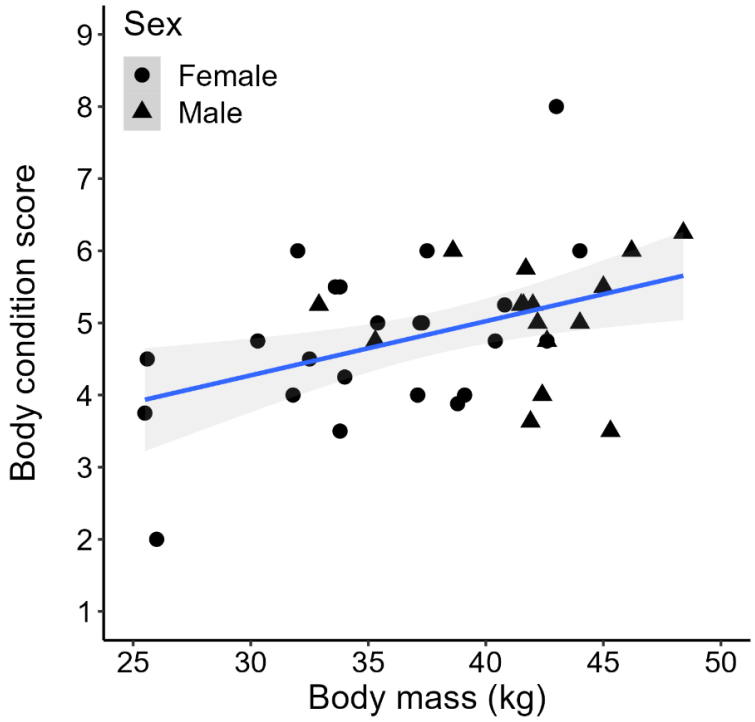

Figure 2: Relationship between body condition score and body mass (in kg) in zoo-housed bonobos (N = 40). A significant positive relationship was found. Individual datapoints are shown, with females represented by circles and males by triangles.

Description of BCSs in the European bonobo population

The mean BCS for our study population was 4.79 ± 1.02 SD (range 2.00-8.00), which did not differ significantly from a normal BCS of 5.00 ($t(75) = -1.813$, $p = 0.074$). The distribution of BCSs was normal ($W = 0.974$, $p = 0.114$), indicating that the European bonobo population showed no skew towards being under- or overweight (Figure 3A). Seventy-eight percent of the study population fell within the normal BCS categories (i.e., BCSs between 4 and 6), while 8% showed a BCS above 6 (i.e., overweight) and 14% showed a BCS below 4 (i.e., underweight). Females showed a wider range of BCSs than males ($mean_{females}$ = 4.68 ± 1.12 SD, $range_{females}$ 2.00 – 8.00; $mean_{males}$ = 4.98 ± 0.81 SD, $range_{males}$ 3.25 – 6.25) (Figure 3B-C).

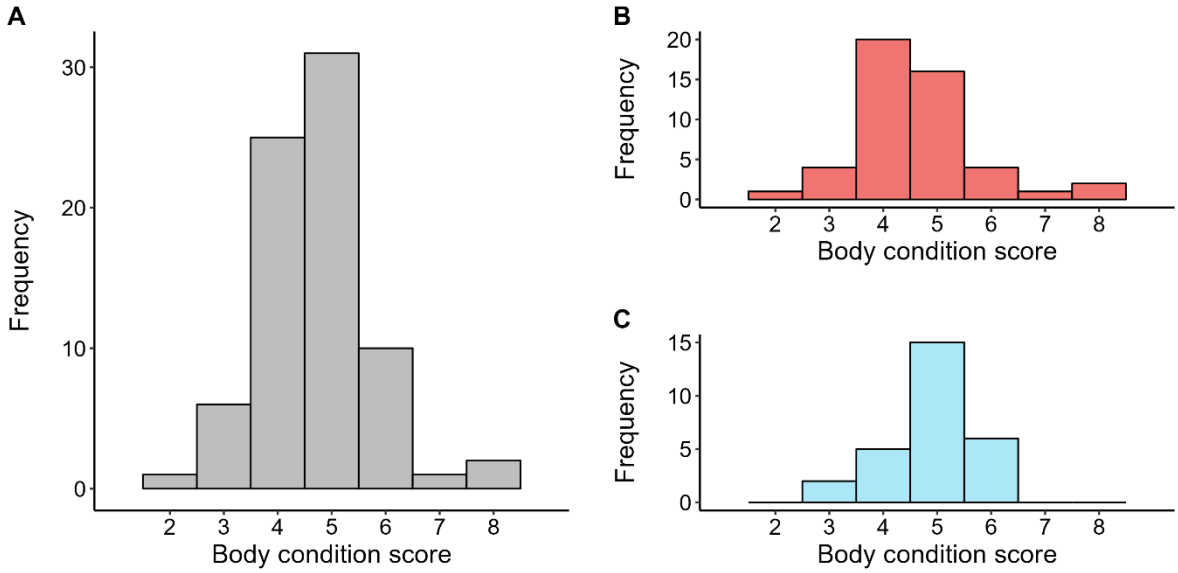

Figure 3: **Absolute frequency distribution of BCSs in our study sample**. (A) Absolute frequency distribution of BCSs in our study sample (N = 76) shows no skew of the European bonobo population towards being under- or overweight. The majority of individuals fell within normal body condition categories (i.e., BCS between 4 and 6). (B) Absolute frequency distribution of BCSs for females (N = 48). (C) Absolute frequency distribution of BCSs for males (N = 28).

External factors influencing BCSs and assessment of heritability

In the model containing all factors including total provided calories (N_{diet} = 61), none of the variables had an influence on BCSs (Supplementary Table S1). A second model was run on the full dataset (N_{all} = 76) excluding total provided calories but including sex, age, and cardiovascular disease. Still, there was no correlation with any of the investigated explanatory variables (Supplementary Table S1). There was no difference among the sexes in mean BCS ($mean_{females}$ = 4.68 ± 1.12 SD, $mean_{males}$ = 4.98 ± 0.81 SD; 95% CI [-0.228 ,0.661], pMCMC = 0.340), no change with age (est. = -0.010, 95% CI [-0.026, 0.006], pMCMC = 0.230), and no effect of cardiovascular disease presence ($mean_{cardiac}$ = 5.51 ± 1.65 SD, $mean_{healthy}$ = 4.74 ± 0.96; 95% CI [-0.359, 1.516], pMCMC = 0.311).

Since no fixed effects explained variation in BCSs we calculated h^2 from an animal model including random effects only. A model including both maternal ID and zoo ID had the lowest DIC value (DIC = 85.64, in comparison to 143.79 for zoo ID only, 102.21 for maternal ID only, and 148.33 for the intercept model without random effects) and was therefore used to assess h^2. Body condition scores showed high and significant heritability, with a h^2 of 0.637 (95% CI [0.256,0.996]). Only small amounts of variation were attributable to maternal effects (0.058; 95% CI [<0.001,0.228]) and group effects (0.041; 95% CI [<0.001,0.147]) (see Table 1).

Table 1: Heritability estimates of BCSs derived from the intercept model (without any random effects) and the best fit model which contained group and maternal ID as random effects. h^2 = heritability, V_A = additive genetic variance, V_R = residual variance, V_{group} = group variance, V_{mother} = variance explained by maternal effects.

	Intercept model	**Best fit model**
DIC	148.33	85.64
h^2	0.612 (95% CI [0.267,0.999])	0.637 (95% CI [0.256,0.996])
V_A	0.698 (95% CI [0.133,1.432])	0.782 (95% CI [0.138,1.497])
V_R	0.402 (95% CI [<0.001,0.758])	0.312 (95% CI [<0.001,0.722])
V_{group}		0.041 (95% CI [<0.001,0.147])
$V_{maternal}$		0.058 (95% CI [<0.001,0.228])

Discussion

In this study, we evaluated the utility of a visual, non-invasive body condition score (BCS) system, initially proposed for chimpanzees (Reamer et al., 2020), in the European zoo-housed bonobo population. By using standardized videos to score BCSs, we found a significant inter-observer agreement showing high repeatability of scores. Body condition scores were also positively correlated with the more traditional body mass measure and showed high heritability (h^2 = 0.637), indicating that a large proportion of the variance in body condition is attributable to genetic relatedness of the individuals. Surprisingly, body condition scores were not associated with other factors like sex, age, obesity-related diseases or total provided calories.

Bonobo BCSs showed a positive correlation with body mass, similar to what has been found in chimpanzees (Reamer et al., 2020). Still, the correlation with body mass was not 'perfect' (see Figure 2), which illustrates the usefulness of the visual BCS system, as individuals of approximately the same body mass could still show large differences in BCSs, largely due to differences in stature or relative fat mass. For example, males that weighed between 41.5 and 42.5 kg (N = 7) would be classified as having the same body condition purely based on body mass, even though they showed highly differentiated body scores ranging from 3.63 to 5.75 due to differences in body frame, muscularity and/or relative fat mass. This shows that the visual BCS system is a more integrative approach, taking relative fat mass into account and therefore providing a more comprehensive body scoring measure than the traditional body mass measure.

As predicted, we also found high levels of heritability (h^2 = 0.637) for bonobo BCSs, indicating that about 64% of the phenotypic variation in body condition is attributable to heritable factors such as genetic or epigenetic variation. This heritability is on the higher end of the spectrum compared to the heritability of BCSs in domesticated species such as cows and sheep. However, our h^2 estimate is along the lines of heritability of other measures of body condition in primates, such as BMI in lab-housed vervet monkeys (h^2 = 0.65; Schmitt et al., 2018) and body mass in male captive baboons (h^2 =

0.62; (Comuzzie et al., 2003)). Moreover, it is in line with the finding that BMI in humans is also heritable, with varying estimates of h^2 depending on the type of study (h^2 varies between 0.24 and 0.90) (reviewed by Elks et al., 2012). It needs to be noted, however, that these studies did not employ animal models to estimate h^2, which hampers direct comparisons.

In contrast to our expectations, we found no difference in BCSs between the sexes in bonobos. In chimpanzees, females had higher average BCSs than males (Reamer et al., 2020), reflecting a general tendency for female chimpanzees to become obese (Lowenstine et al., 2016; Nunamaker et al., 2012). In bonobos, females tend to show higher relative fat mass than males (Zihlman & Bolter, 2015) and typically occupy high ranks and therefore have primary access to highly preferred food items (Vervaecke et al., 2000; White & Wood, 2007), which could lead to higher BCSs. However, we found no sex-difference, which could be explained by the fact that bonobos do not show absolute female dominance, with some adult males obtaining higher ranks than some females in the group (Stevens et al., 2007), or by the fact that individuals simply have plenty of access to food, cancelling out potential effects of food competition on overall body condition. Moreover, even though female bonobos have higher tendencies to accumulate fat mass compared to males, fat mass is still relatively low in bonobos when compared to other great apes such as gorillas, orangutans and humans (Morbeck & Zihlman, 1988; Zihlman & Bolter, 2015; Zihlman & McFarland, 2000). So, if sex-differences in relative fat mass are present, they might be too subtle to notice using a visual BCS system in this species.

We also did not find any changes with age in BCSs in our study sample. Although we expected an increase in BCSs among bonobos, as in a previous study in chimpanzees with a similar age distribution (Reamer et al., 2020), BCSs appear to remain relatively stable with age in our bonobo population. However, the relationship between age and body condition seems to be complex, especially in older age categories. Generally, great apes show increased risk of obesity with age, but frailty is also commonly seen in geriatric apes (Lowenstine et al., 2016). Similarly, in humans, BMI increases with age up until about 60 years old, whereafter BMI declines (Elia, 2001), with an increasing

occurrence of frailty in the elderly population (Fried et al., 2004). In zoo-housed bonobos, diet can be flexibly adjusted to maintain a healthy body condition for elder individuals, obscuring any age-effects on BCSs. Moreover, in humans, this research has been done in a longitudinal rather than a cross-sectional fashion, and this might also explain the absence of any age-effects in our study. Given that more than 60% of the variation in BCSs is attributable to an individual's genetic build, individuals of the same old age are not necessarily expected to show similarly low BCSs. Instead, BCSs are expected to show changes within an individual as they age rather than consistently differing between individuals of different age classes. Therefore, continuous long-term longitudinal follow-ups of individual BCSs are preferred to infer biologically meaningful changes with age within individuals.

We did not find an association between BCSs and the occurrence of obesity related diseases, even though this pattern was found in chimpanzees (Reamer et al., 2020), which is likely due to the low occurrence of obesity-related diseases in our sample. No bonobos in our sample were known to suffer from arthritis, diabetes or hypertension, and only five bonobos (6.6% of the study population) were diagnosed with cardiovascular disease. While these individuals had on average higher BCSs than the rest of the study sample ($BCS_{cardiac}$ = 5.50 ± 1.65 SD; $BCS_{healthy}$ = 4.71 ± 0.96 SD; see Supplemental Dataset 1) and included the highest BCS recorded in our sample (ID133 with a BCS of 8.00), the difference was not significant. As monitoring of obesity-related diseases is often done opportunistically in zoos, it is likely that some cases remain undiagnosed. Regular screening for cardiovascular disease using echocardiograms (Murphy et al., 2018) and markers in blood and urine (e.g., Edes & Brand, 2021; Ndrepepa, 2018; Videan et al., 2009) could provide a better image of the presence of cardiovascular disease in the bonobo population. It is unlikely that age plays a role in the low occurrence of obesity-related disease, as the age distribution between our study and Reamer et al. (2020) is highly similar, with a similar amount of elderly individuals older than 40 (N = 13 and 14, respectively). Regardless, the rarity of obesity-related diseases is in line with the distribution pattern of BCSs around a normal level of relative fat mass in our bonobo population, with the average BCS being around 5.00. This means that the bonobo population is not skewed towards being overweight, likely resulting in overall fewer

449 health problems. In chimpanzees, the population did show a skew towards obesity and as a result, a
450 higher frequency in cases (Reamer et al. 2020).

451 Previous work in zoo-housed bonobos reported changes in body mass and urinary C-peptide
452 levels, a measure for an animal's energy balance, following experimental reductions and increases in
453 energy content of the diet (Deschner et al., 2008). However, we found no influence of total provided
454 calories on bonobo BCSs. There are a couple of limitations that need to be taken into account when
455 interpreting these results. Given that we relied on dietary information sheets provided by zoos to
456 estimate the caloric content of the diet, true caloric values may differ for a number of reasons. Food
457 items may opportunistically be substituted with enrichment or alternative food items depending on
458 market availability, which are often high energy food items such as nuts. Caloric values for food items
459 reported in literature or by the manufacturer may also differ from true caloric values, possibly leading
460 to suboptimal calculations of dietary intake. Moreover, diets will also differ in the composition of
461 macronutrients (e.g. fiber, fat, protein, carbohydrates). As these macronutrients have different
462 metabolic roles, diets with similar energy content but different macronutrient composition might still
463 show differences in energy yield during digestion (reviewed in Martinez et al., 2014), and as a
464 consequence might result in varying body condition. Dietary data were also considered at the group-
465 level, but could show considerable between-individual variation in caloric intake levels that obscures
466 group-level variation: even though zoos have a good idea of what the diet is of the group as a whole,
467 individuals in the same zoo fed on the same diet could still have varying food intakes. This could depend
468 on factors such as individual food preference (Verspeek & Stevens, 2020), feeding priority due to their
469 place in the dominance hierarchy, and intake of food that is not provided actively by the zoo, such as
470 browse that is often available ad libitum in outdoor enclosures and that is thus missing from dietary
471 sheets. However, previous work in chimpanzees showed that even when all individuals were housed
472 in the same institution with similar food access, BCS values still range from 5 to 9, which indicates that
473 dietary intake may not be the primary driver of variation in captive ape BCSs (Reamer et al., 2020).
474 Similarly, in our study sample, we found that bonobos housed at the same zoological institute who

475 shared the same diet, still showed considerable variation in BCSs, ranging from underweight (i.e., BCS
476 below 4) to overweight (i.e., BCS above 6) (see Supplemental Dataset 1).

477 A large proportion of the between-individual variance in BCSs currently also remains
478 unexplained (about 26%). A potential contributing factor is an individual's behavior, as low activity
479 levels have been associated with high relative fat mass in long-tailed and rhesus macaques (Bauer et
480 al., 2012; Wolden-Hanson et al., 1993; Zijlmans et al., 2022), although low activity might also be a
481 consequence of being overweight, rather than a cause (Zijlmans et al., 2022). Another potential factor
482 is the gut microbiome, as it is known to influence how much energy is harvested from the diet and is
483 highly individualized, possibly leading to BCS differences among individuals that are fed the same diet.
484 The gut microbiome has already been shown to impact BMI in humans (e.g., Dong et al., 2020;
485 Turnbaugh et al., 2006) and fat and body mass in captive long-tailed macaques (Newman et al., 2021;
486 Sawaswong et al., 2021).

487 To conclude, our results indicate that a visual BCS system offers a practical, reliable, and non-
488 invasive tool to measure body condition of bonobos. In contrast to traditional body condition
489 measurements, no sedation or training is required and BCSs provide a more inclusive estimate of body
490 condition. Due to the large genetic basis driving BCS variation, individual longitudinal BCS collection is
491 likely more informative for welfare and health assessment as opposed to between-individual
492 comparisons. Longitudinal BCS monitoring could inform management decisions regarding dietary
493 changes, follow-ups after zoo transfers, or the need for testing for obesity-related diseases. For
494 example, body condition could be scored before and after a dietary change using a visual BCS system
495 by caretakers, veterinarians, researchers, and other zoo staff, either using live scoring (e.g., as in
496 Reamer et al (2020)) or by collecting videos. Due to its practicality, the BCS system can also be applied
497 in wild populations. It is currently unclear whether the high level of BCS heritability is due to the highly
498 standardized and controlled environment in which zoo-housed primates are managed. For example,
499 the high heritability in the zoo-housed bonobo population might be caused by the small founder base,

leading to high levels of kinship within the population, possibly inflating heritability estimates. It is possible that in wild populations, the influence of environmental factors such as diet and variation in food availability on BCSs might be higher, resulting in lower heritability estimates. Selection against certain BCSs might also be higher in wild populations compared to captive populations, which would influence heritability estimates. Future systematic comparisons of BCS heritability in both wild and captive settings would aid to further unravel the environmental and genetic drivers of body condition variation in primates.

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Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

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